

Extreme host specificity by *Microdon mutabilis* (Diptera: Syrphidae), a social parasite of ants

G. W. Elmes*, B. Barr†, J. A. Thomas and R. T. Clarke

Furzebrook Research Station, Institute of Terrestrial Ecology, Wareham, Dorset BH20 5AS, UK

Larvae of the syrphid fly *Microdon mutabilis* are social parasites which live up to two years, feeding on ant brood in nests of *Formica lemani* ants. We questioned why *M. mutabilis* is extremely localized when its host is widespread and abundant. Like endoparasitic diseases, social parasites must penetrate formidable defences before ‘infecting’ their hosts. This occurs during the egg stage of *M. mutabilis*: females are sedentary and oviposit at *F. lemani* nest entrances, which workers treat as part of their nest, leaving the thin-shelled eggs vulnerable to attack for 10–14 days before hatching. We describe experiments which show a strong maternal effect in *M. mutabilis*. New-laid eggs had > 95% survival when introduced to the individual ant colony that reared each mother fly or to its close neighbours, but survival declined as a sigmoidal logistic function of distance from the mother nest, with *F. lemani* colonies from 2 and 30 km away killing 80 and > 99% of eggs, respectively, within 24 h. Attacks on eggs also increased in proportion to the delay before introduction to laboratory nests. We suggest that they may be coated with a mimetic chemical disguise that lasts for three to four days after oviposition. The results indicate extreme local adaptation by an *M. mutabilis* population not simply to one species of host, but to an individual host population and possibly to local strains or family groups within an *F. lemani* population. This conclusion is discussed in terms of virulence, transmission and coevolution in parasitic diseases.

Keywords: myrmecophily; host specialization; oviposition; maternal effect; coevolution

1. INTRODUCTION

Ants are the quintessential keystone species among the terrestrial invertebrates. Their abundant colonies dominate most terrestrial ecosystems at their scale and play a major role in determining the biodiversity of communities (Hölldobler & Wilson 1990; Wilson 1990). In addition to their direct impact on other species, ant colonies provide habitats for a large number of microbial and invertebrate species (myrmecophiles), which possess complex adaptations for coexisting with ants (Kistner 1982; Hölldobler & Wilson 1990; Dettner & Liepert 1994). Most myrmecophiles are commensals or mutualists, but a smaller number of species from a wide range of taxa represent social parasites, which infiltrate ant social systems to exploit the resources ants gather into their nests.

Social parasites tend to be more specialized than mutualistic myrmecophiles. For example, their secretions may mimic the complex recognition pheromones of their host ant species whereas those of mutualists consist mainly of general ant foods (Hölldobler & Wilson 1990; Dettner & Liepert 1994). However, a trade-off can occur in the evolution of a social parasite between increased specialization to improve its penetration of host societies and a reduction in the range of hosts it can exploit (Thomas & Elmes 1998). The ecological consequences of

few forms of social parasitism have been studied. Certain relationships, such as those between *Maculinea* butterfly larvae and *Myrmica* ants, are so intimate that the social parasite and its hosts form a ‘community module’ of species whose population dynamic interactions are largely divorced from the other species within their biotope (Thomas *et al.* 1998). These specialized systems have already proved useful for testing population ecological theory (Hochberg *et al.* 1996; Clarke *et al.* 1997).

Here we describe a different ant–social parasite system to which ideas about host–parasite relationships, virulence and coevolution might usefully be extended (e.g. Toft *et al.* 1991; Read & Harvey 1993; Thompson 1994). We examine a key question concerning social parasites: why—with a few exceptions—are they so rare in comparison to their hosts? One partial explanation may be the need for another (sequential) host to coexist with the host ants, such as the second ant species used by *Atemeles* beetles (Hölldobler & Wilson 1990) or the initial larval foodplant of *Maculinea* butterflies (Thomas *et al.* 1998). However, many social parasite species have no secondary host and yet are no less rare.

The *Red data book* syrphid fly *Microdon mutabilis* (L.) exemplifies this paradox (Shirt 1987). It lives for up to two years, from egg to eclosion, in a host ant colony, encountering other potential enemies only during a brief adult period lasting *ca.* 2% of its lifespan. Its known hosts in Europe encompass six species from three genera of ants, including some of the most abundant and widespread ants on the continent (Donisthorpe 1927). In contrast, *M. mutabilis* forms extremely localized, small

*Author for correspondence (g.elmes@ite.ac.uk).

†Present address: Logierait School House, Ballinluig, Pitlochry PH9 0LG, UK.

populations that typically persist for many generations on the same small (often < 0.1 ha) isolated patches. Stubbs & Falk (1983) suggested that *M. mutabilis* may parasitize different ant species in different parts of its range. Our unpublished observations support this view. We have found it in west Scotland exclusively with *Formica lemani* Bondroit and in south England only with one species of *Myrmica*. We have also observed that female *M. mutabilis* seldom disperse more than a few metres from their original (natal) host nest, that females oviposit mainly in that nest and its immediate neighbours (also recorded by Donisthorpe (1927)) and that captive eggs appear to be more acceptable to workers from the mother's natal colony than to those from other colonies. We therefore hypothesized that *M. mutabilis* might resemble some macroparasites (e.g. Lively 1989; Dybdahl & Lively 1996) in being adapted not only to a single host species on a regional scale but to particular populations—or even to family groups of ant nests within populations—on a local scale. This paper reports the results of laboratory experiments designed to test the null hypothesis that *M. mutabilis* eggs are equally acceptable to all host-species' colonies, regardless of their geographical distance from the mother's natal nest.

2. MATERIAL AND METHODS

(a) *The Microdon system*

More than 350 species of *Microdon* Meigen are known from all zoogeographic regions (Duffield 1981). In temperate zones, larval *Microdon* are found almost exclusively in the nests of ants although they live with other social insects in the tropics (Akre *et al.* 1973). Myrmecophily by *Microdon* has been studied in detail in only a few, mainly nearctic, species (Andries 1912; Duffield 1981; Garnett *et al.* 1985, 1990; Howard *et al.* 1990; Stanley-Samuelson *et al.* 1990; Barr 1995). Most authors concentrate on the second to third instar larvae, which inhabit brood chambers and eat ant brood (e.g. Greene 1955). These stages are protected by a thick hemispherical dorsal cuticle, which is both difficult for ants to bite and well-endowed with glands that secrete mimetic semiochemicals (Howard *et al.* 1990; Stanley-Samuelson *et al.* 1990; Dettner & Liepert 1994).

Donisthorpe's (1927) and Barr's (1995, unpublished data) studies of *M. mutabilis* revealed similarities and differences to the nearctic species. As in other species (Andries 1912; Akre *et al.* 1973), females lay up to 200 eggs in the laboratory, but probably many fewer in the wild. The chorion of the eggs has a distinctive surface structure (Garnett *et al.* 1990). *Microdon mutabilis* deposit eggs in batches of three to six eggs on soil at the entrances of *F. lemani* nests; nest soil is essential for stimulating oviposition. Social parasites generally experience heavy mortalities while penetrating and integrating with their host ant colonies (e.g. Hölldobler & Wilson 1990; Dettner & Liepert 1994). For *M. mutabilis*, the 14 day egg stage is critical, because *F. lemani* workers treat nest entrances as part of their colony and, indeed, kill many of the thin-shelled eggs (see § 3). The newly hatched larva is flatter and more mobile than later instars. It is not transported by host workers; rather it crawls into the nest and, like some nearctic species, it hides inside a pupal cocoon, feeding on the pupa (Garnett *et al.* 1985). However, unlike the nearctic species, there is no evidence that *M. mutabilis* larvae are attractive to their hosts. Ants are generally indifferent to older larvae, but if a worker touches or bites one they appear unattractive, repellant or even toxic (Barr 1995).

(b) *Experimental stock*

Stock originated from an *ca.* 18 ha site situated each side of a 1 km track beside Loch Frisa on the Isle of Mull, Scotland. In April 1997, we estimated that *ca.* 25% of the 300–400 nests of *F. lemani* present contained *M. mutabilis* ($n=130$). To avoid damaging the population, sampling was restricted to the collection of all third instar *M. mutabilis* larvae found at the surface of 30 nests, representing 33–40% of the 1997 emergence. Eight of these nests (chosen at random) were excavated to provide test ants and nest soil. To test more distant colonies, two additional nests, which contained no *Microdon*, were excavated from the periphery of this site, as were two *F. lemani* nests from the Isle of Coll, > 30 km away, where *M. mutabilis* is unknown. Distances between nests on Mull were measured (± 1 m).

(c) *Laboratory procedure*

The ants were placed in shallow boxes (75 mm \times 135 mm \times 10 mm) with glass lids and were kept in the dark at 22 °C, with ample food and water. *Microdon* pre-pupae were removed and placed singly in small plastic boxes with water pads. After emergence, a female and male (whenever possible from different host nests) were placed in a moist but aerated box lined with tissue; pairing was stimulated by warmth and light. After 36–48 h, each mated female was transferred to an oviposition box with the same environmental regime and containing soil taken at random from one of the ant colonies. Eggs were quickly removed to coded microscope slides fitted with aluminium rings and were covered with cover slips to prevent desiccation. We thus knew the source of soil and the mother and father of each egg batch. After becoming pre-pupae, neither parent had any contact with ants other than indirectly via the soil in which females oviposited. Twenty-six successful pairings were achieved, resulting in zero to > 150 eggs per female.

(d) *Experimental procedure*

The basic test of the acceptability of *M. mutabilis* eggs to host ant workers consisted of three matched trials, called a triplet. In each triplet, batches of ten sibling eggs were introduced to the foraging arenas of each of three test colonies, consisting of *ca.* 100 workers and two queen *F. lemani*. Each female *M. mutabilis* was tested three times with different triplets, requiring a minimum of 90 eggs. Only eight females laid enough eggs to meet the experimental design. The eggs could be 1–6 days old before being tested, but we ensured that every egg in a triplet was the same age and viable. Whenever possible, each triplet compared the response of a test colony from the female's natal nest (or a close neighbour) to one from *ca.* 500 m away and to another from the most distant nests. Thirty such triplets (in two cases 'triplets' consisted of only two nests) were tested using different permutations of the same 12 test nests, giving a total of 88 trials. Every triplet was carried out as a blind experiment, whereby the scientist who introduced eggs and recorded the outcome had no knowledge of the origins of the eggs or ants being tested.

In the first 14 triplets, nests were observed under red light, to confirm that the eggs were always found and examined by workers and to record the ants' reactions to them. The workers exhibited a wide range of behaviours which we grouped into six classes of increasing aggression. Class 0 was when ants ignored eggs and treated them as part of the background clutter of the nest. Intermediate levels included close examination and picking an egg up and carrying it a short distance (class 1) and threatening to spray acid, threat with open mandibles and/or attempts to bury the eggs (class 2 when one or two workers

reacted this way and class 3 when more did). More extreme aggression ranged from spraying eggs with acid and biting by some workers (class 4) to concerted attack, with the whole colony becoming agitated (class 5). In all trials the eggs were classed after 24 h as surviving (undamaged), damaged (usually a punctured chorion causing the embryo to die within a few days) or destroyed (completely cut up, with often no trace remaining). Eggs were not reused.

(e) Statistical analysis

The proportion of eggs surviving 24 h (SURVIVAL) in each trial was the dependent variable against which the effects of all experimental factors were tested. To test the original null hypothesis, we simply ranked the three trials in each triplet (1–3) according to the distance of the test nest from the mother's natal nest (DIST♀) and made a Friedman non-parametric two-way (triplet × DIST♀) ANOVA test on survival. Other factors which might affect SURVIVAL were age of the eggs (AGE), the natal nest of the mother and of the father and the distances of the test nest from the natal nest of the father (DIST♂) and from the nest which provided the soil in which the eggs were laid (DISTSOIL). Trivariate plots suggested nonlinear effects and interaction of these factors with sigmoidally shaped survival response curves (as is usual for survival data). Regression models were therefore based on a logistic binomial survival response, made linear by a logit transformation (LSURVIVAL = $\log_e(P/(1-P))$, where $P = \text{SURVIVAL}$). We used a generalized linear model (GLM) approach, estimating parameters by maximum likelihood, using the BLOGISTIC procedure in MINITAB®. The effects of additional factors were assessed by changes in deviance χ^2 goodness-of-fit statistics (McCullagh & Nelder 1989). All distance variables had highly skewed distributions and were \log_e transformed (log zero distances set to 0) because this always gave improved model fits.

3. RESULTS

(a) Survival

Despite being very variable, %SURVIVAL varied significantly within triplets according to the rank of DIST♀ (Friedman two-way ANOVA: $\chi^2_2 = 12.9$ and $p = 0.002$) with mean %SURVIVAL (\pm s.d.) of $54 \pm 37\%$ for the nest closest to the mother's natal nest, $32 \pm 41\%$ for the next closest and $11 \pm 24\%$ for the furthest. Much of the variability in survival within ranks was due to variation in DIST♀, for example nearest nests had DIST♀ = 0 m (the mother's natal nest) in some triplets and DIST♀ of > 400 m in a few others, while the furthest nests had DIST♀ of < 100 m in some cases and 30 km in others. Although this result provided *prima facie* evidence to reject our null hypothesis, DIST♂ and DISTSOIL also correlated with SURVIVAL (Spearman's rank correlation: $r_s = -0.47$ and $p < 0.001$ and $r_s = -0.53$ and $p < 0.001$, respectively). Therefore the subsequent analysis was aimed at discriminating between the relative importance of these factors.

Logistic regression model fits, based on the 88 trials, showed that LogDIST♀ had the most effect on SURVIVAL (deviance $\chi^2_1 = 245.3$ and $p < 0.001$). Although the relationship appeared very variable (figure 1a), it became much clearer when egg age was taken into account (table 1 and figure 1b–1d). Statistically significant partial effects were exhibited by both LogDIST♀

(deviance $\chi^2_1 = 242.1$ and $p < 0.001$) and AGE (deviance $\chi^2_1 = 85.7$ and $p < 0.001$) when combined in GLM. There was also a significant interaction which was best represented by the simple additional term AGE × LogDIST♀ (deviance $\chi^2_1 = 28.2$ and $p < 0.001$); incorporating other nonlinear effects of AGE and LogDIST♀ did not significantly improve the model. The proportion, P , surviving (superimposed in figure 1) was estimated from the following best fit equation (\pm s.e. of coefficients) for these two factors:

$$\begin{aligned} \text{LSURVIVAL} = & 5.08_{\pm 0.54} - 0.889_{\pm 0.094} \text{LogDIST♀} \\ & - 1.35_{\pm 0.18} \text{AGE} \\ & + 0.166_{\pm 0.033} \text{AGE} \times \text{LogDIST♀}, \quad (1) \end{aligned}$$

where the proportion surviving $P = \exp(\text{LSURVIVAL}) / (1 + \exp(\text{LSURVIVAL}))$.

There was no statistical evidence that the distance from the father's nest (LogDIST♂) had any effect upon SURVIVAL (deviance $\chi^2_1 = 1.39$ and $p = 0.24$) other than through its high correlation with LogDIST♀ ($r = 0.78$ and $p < 0.001$). This chance correlation in our experiment was due to the lack of control over which pairs would provide sufficient eggs and to the limited supply of *Microdon* adults (see §2). However, it is important to note that the effect of both LogDIST♀ and AGE were almost unchanged and still highly significant ($p < 0.001$) when LogDIST♂ was included in the model.

The consequence of the most distant nests (DIST♀ > 1 km) containing no *M. mutabilis* when collected (figure 1, open circles) was tested by adding a dummy variable (MM, value 1 when *Microdon* was present and 0 when absent). This indicated an additional tendency for lower survival in test colonies where *Microdon* was absent (coefficient 1.78 ± 0.33 and $p < 0.001$), besides that due to AGE and LogDIST♀. However, MM did not unduly influence the statistical relationships (coefficients) with AGE and LogDIST♀, which remained significant ($p < 0.001$) when restricted to *F. lemani* colonies which contained *Microdon* when collected (figure 1, solid circles):

$$\begin{aligned} \text{LSURVIVAL} = & 5.25_{\pm 0.62} - 0.841_{\pm 0.115} \text{LogDIST♀} \\ & - 1.47_{\pm 0.21} \text{AGE} \\ & + 0.180_{\pm 0.041} \text{AGE} \times \text{LogDIST♀}. \quad (2) \end{aligned}$$

It was not possible to examine individual maternal and paternal effects because males were paired with only a single female. However, we detected residual variation in SURVIVAL between the eight pairs (deviance $\chi^2_7 = 26.1$ and $p < 0.001$) but the importance of AGE and LogDIST♀ was unaltered. The effect of the origin of soil used for oviposition (LogDISTSOIL) also had a statistically significant partial effect (deviance $\chi^2_1 = 14.1$ and $p < 0.001$), indicating that the negative rank correlation between SURVIVAL and LogDISTSOIL (above) might represent a real additional effect.

Thus the best-fitting overall model to the observed survival data, incorporating the effects of all statistically significant ($p \leq 0.05$) factors, was the logistic relationship

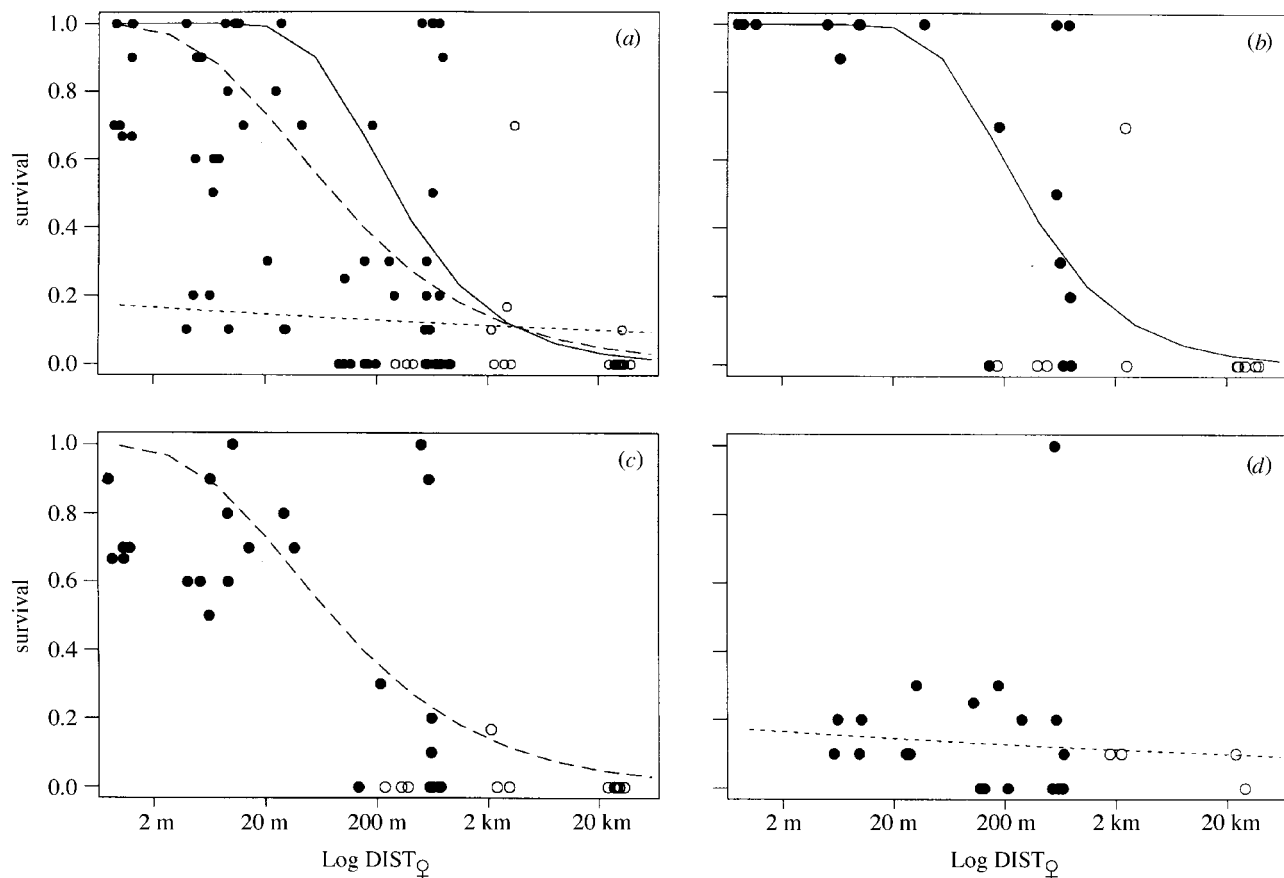


Figure 1. The proportion of *M. mutabilis* eggs surviving 24 h after introduction into a test colony of *F. lemni* ants plotted against the distance ($\text{LogDIST}_{\text{♀}}$) of the source nest for the tested colony from the female's natal host nest. To distinguish overlapping points, a small amount of random jitter has been added to the distance values. Open circles indicate *F. lemni* test colonies which had not previously reared *Microdon*. Lines indicate the fit (equation 1) for 1-day-old (solid), 2–3-days-old (dashed) and 4–6-days-old (dotted) eggs. (a) All data, (b) 1-day-old eggs, the situation when eggs are laid in the wild and (c) 2–3-days-old and (d) older eggs.

Table 1. Survival after 24 h of *M. mutabilis* eggs placed in laboratory test colonies of *F. lemni* representing nests originally situated at different distances ($\text{DIST}_{\text{♀}}$) from the mother's natal nest

(Survival (%surv) is averaged (n =number of batches of ten eggs tested) within 20 classes formed by grouping $\text{DIST}_{\text{♀}}$ geometrically (0 when tested against mother's natal nest) against the age of the eggs at the start of the test (AGE).)

| day | $\text{DIST}_{\text{♀}}$ | | | | | | | | | |
|-----|--------------------------|--------|----------|--------|-----------|--------|----------|--------|----------|--------|
| | 0 m | | 1–100 m | | 101–800 m | | > 800 m | | all | |
| | <i>n</i> | % surv | <i>n</i> | % surv | <i>n</i> | % surv | <i>n</i> | % surv | <i>n</i> | % surv |
| 1 | 3 | 100 | 5 | 98 | 12 | 31 | 7 | 10 | 27 | 46 |
| 2 | 2 | 80 | 6 | 75 | 7 | 14 | 4 | 0 | 19 | 37 |
| 3 | 3 | 68 | 4 | 68 | 6 | 25 | 6 | 3 | 19 | 34 |
| 4 | — | — | 3 | 20 | 7 | 25 | 2 | 5 | 12 | 20 |
| 5–6 | — | — | 4 | 13 | 5 | 5 | 2 | 10 | 11 | 9 |
| all | 8 | 83 | 22 | 60 | 37 | 22 | 21 | 6 | 88 | 33 |

$$\begin{aligned}
 \text{LSURVIVAL} = & 5.86_{\pm 0.72} - 0.827_{\pm 0.117} \text{LogDIST}_{\text{♀}} \\
 & - 1.37_{\pm 0.21} \text{AGE} \\
 & + 0.172_{\pm 0.040} \text{AGE} \times \text{LogDIST}_{\text{♀}} \\
 & - 1.38_{\pm 0.38} \text{MM} \\
 & - 0.125_{\pm 0.048} \text{LogDISTSOIL} + \text{PAIR},
 \end{aligned}
 \tag{3}$$

where pair effects (PAIR) range between -1.02 and 1.17 .

(b) Behaviour of the ants

Ants soon discovered all the introduced *Microdon* eggs and never appeared to find them attractive. The best outcome for the egg was to be superficially examined and then ignored. All other responses were aggressive. Unsurprisingly, there was a strong negative Spearman rank correlation between the survival of eggs during the 24 h period and the degree of aggression exhibited in the first hour (figure 2a; $r_s = 0.79$, $p < 0.001$ and $n = 42$).

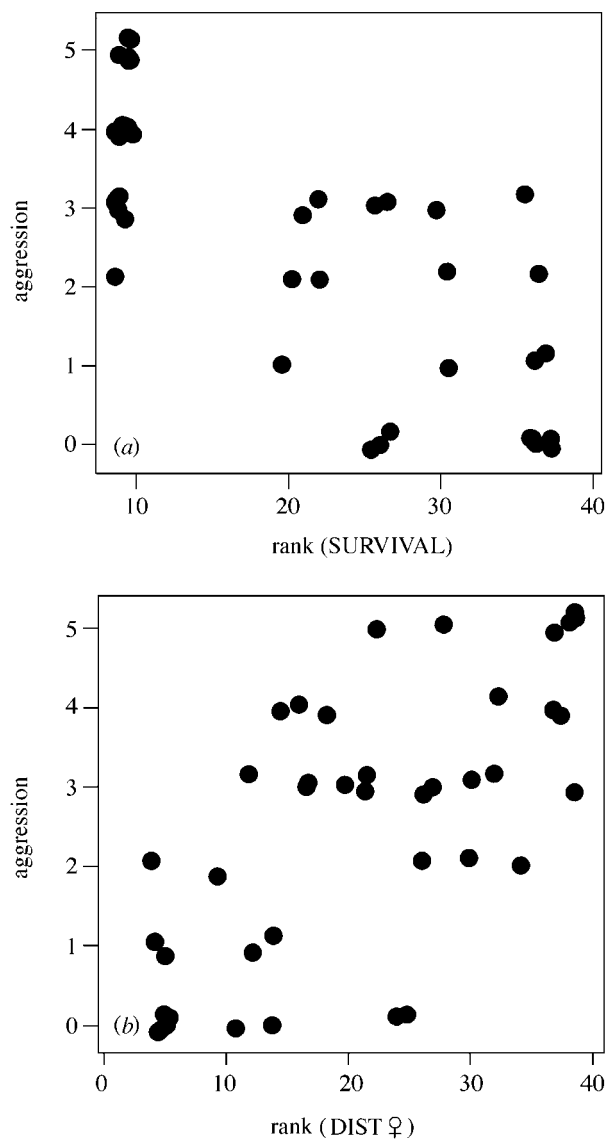


Figure 2. Aggression (ranked 0–5, none to strong antagonism) shown to eggs of *M. mutabilis* during their first hour with *F. lemani* test colonies (first 14 triplets) plotted against (a) the rank (SURVIVAL) after 24 h in the nest and (b) the rank (DIST♀)—distance of the tested colony from the mother's natal nest.

Consequently, the relationship between SURVIVAL and aggression was mirrored by a significant rank correlation between aggression and LogDIST♀ (figure 2b; $r_s = 0.69$, $p < 0.001$ and $n = 42$).

4. DISCUSSION

These results indicate that *M. mutabilis* displays extreme local host specificity during oviposition. There was a major nonlinear decrease in the survival of its eggs (equation (1)) with increasing geographic distance from the maternal nest (table 1 and figure 1). This operated over remarkably short distances and held true when analyses were restricted to *F. lemani* colonies that had recently reared *M. mutabilis* (equation (2)) and when all the other factors were included (equation (3)). It is important to note that the pattern in survival was multi-directional. Eggs from nest X_i always survived well with

neighbouring nests but poorly with any distant nest X_j and vice versa, irrespective of their locations within the 18 ha site. Thus, the results cannot be explained by undetected environmental gradients that might make *F. lemani* intrinsically less suitable for *M. mutabilis* in certain subareas.

We suggest that the most probable explanation for these results is that the relatedness of *F. lemani* colonies diminishes with distance on Mull and that, in order to achieve social integration, *M. mutabilis* eggs mimic the recognition cues employed by their mother's host colony so closely that they have a low probability of survival in more distant *F. lemani* colonies. If so, the mechanism might be odour. Subtle variation in the chemical composition of pheromones is the main cue used by ant colonies to distinguish between kin neighbours (which are accepted), unrelated conspecifics (which are attacked) or intermediates. It is also almost axiomatic that social parasites employ chemical mimicry to penetrate their hosts' defences, although tactile, behavioural and acoustical cues may supplement it (Hölldobler & Wilson 1990; Dettner & Liepert 1994).

We suspect that the chorion of a newly laid *M. mutabilis* egg contains a semiochemical which mimics the odour recognition signal of the maternal ant colony. We obtained no direct evidence, but the following points are perhaps corroborative.

- (i) The larva of a nearctic species is known to synthesize mimetic chemicals of its host (Howard *et al.* 1990).
- (ii) The decline in acceptability of healthy eggs as they age (figure 1) is consistent with the denaturing of a volatile non-renewable chemical coating, whereas tactile (morphological) mimicry is unlikely to alter with age. The fact that the most distant colonies tested accepted only the oldest eggs (figure 1d) also suggests that the cues which provoke a hostile response diminish over time.
- (iii) Other (behavioural or acoustical) cues employed by social parasites are unlikely to function in eggs.

The origin of any chemical disguise is likely to be maternal, because the low survival of older eggs when introduced to nests makes it unlikely that it is secreted by the chorion. It is also unlikely to have been absorbed from the soil because other myrmecophiles that absorb odour take several days to acquire sufficient to become integrated with their host's society (Hölldobler & Wilson 1990; Dettner & Liepert 1994), whereas in our experiment eggs were only in contact with ant nest soil for a few hours. However, this could explain the minor (but significant) effect of LogDISTSOIL (equation 3).

Little is known about the genetics or demography of *F. lemani* populations. Our field observations confirm Collingwood's (1979) observation that *F. lemani* colonies are both more frequently polygynous (multiqueened) and more apt to reproduce by colony fission than those of its close relative *Formica fusca* L. and that it tends to live in many small nests rather than a few large ones (polydomy). Polygyny, polydomy and colony fission have major consequences for genetic structure within and between ant populations (Levings & Traniello 1981; Keller 1993). Colony fission results in neighbouring nests being more closely related than more distant ones on the

same site, an effect that is reinforced in polygynous species of ant by the recruitment of daughter queens back into their societies. These three traits can lead to complex relationships at a very local scale (Seppa & Pamilo 1995). They enable a species to dominate stable habitats and often result in 'super-colonies' of such closely related colonies occupying nearby nest sites that it may be difficult to determine where one colony ends and the next begins (Rosengren *et al.* 1993). Such behaviour could produce structured variation within the host population, consistent with the pattern in figure 1, on long-lived, ecologically stable sites such as that studied on Mull.

Whatever mechanism is involved, *M. mutabilis* clearly exhibits a strong maternal effect over egg survival. This could be genetic or environmental in origin (de Jong 1998). If wholly genetic, it is surprising that no influence of the father was detected in the experiment. If environmental, it is hard to explain why *M. mutabilis* is so very localized and rare, since the offspring of every migrating female whose eggs overcame the initial obstacle of acceptance by a distant *F. lemani* colony would be perfectly adapted to local ant societies from the first generation onwards; genetic adaptation might take several generations to evolve, during which time extinction becomes probable. Nevertheless, even if the maternal effect were environmental, the fact that only 6% of new-laid *M. mutabilis* eggs survived in *F. lemani* colonies when DIST♀ was >1 km and none survived in *F. lemani* colonies 30 km away is perhaps sufficient to select for the low dispersal observed for adult females (see § 1). Furthermore, there was some evidence of habituation by host colonies, in that ants from colonies with no previous experience of *M. mutabilis* killed slightly more eggs than expected in comparison with those colonies which had previously reared them. Thus, infestation of new *F. lemani* populations may be a rare event.

This system has interesting parallels with diseases. Each *F. lemani* colony is analogous to an individual sedentary organism, its super-colonies resemble 'clones' of organisms and *M. mutabilis* represents a disease parasite which reduces the fitness of its host. *F. lemani* also resembles a host which can reproduce asexually (polygynous strains of *F. lemani* which spread mainly by colony fission) and sexually (monogynous strains which found new colonies from single queens). Host-parasite theory predicts local adaptation to isolated host populations (Lively 1989) but it is not clear whether coevolution can lead to a specialization on clones within a host population (Dybdahl & Lively 1996). Our result suggests that this relationship might exist between the populations of *M. mutabilis* and *F. lemani* on Mull. Coevolutionary dynamics should lead to parasites becoming more damaging (virulent) to sympatric hosts than to allopatric hosts (Ebert 1994). Our result follows this prediction on a relatively small geographic scale. Similarly, Imhoof & Schmid-Hempel (1998) found a tendency for increased virulence in a bumblebee microparasite on a local scale but not on a regional scale; we suspect that, when tested, our result will hold over the larger scale.

More widely in Europe, *M. mutabilis* parasitizes several species from three ant genera (Donisthorpe 1927), although we have never found it using more than one host species in any region. It is possible that host transfer by

social parasites could generate speciation analogous to that following host transfer by some macro-parasites of mammals (e.g. by strains of *Schistosoma*; Coombes 1991). With current knowledge, we cannot determine whether the taxonomic status of *M. mutabilis* resembles that of *Maculinea alcon* Denis & Schiff, which exploits different ant species in a gradient across its range and for which evidence of cryptic speciation between populations is accumulating (Gadeberg & Boomsma 1997; Thomas & Elmes 1998). On the other hand, the geographic mosaic theory of coevolution predicts specialization by parasites on different hosts and unique interactions between the same species pairs in different parts of their range, without necessarily leading to speciation (Thompson 1994). These possibilities could be tested by comparing host specificity in other populations of *M. mutabilis*. Apart from their theoretical interest, the results may have important implications for the conservation of this valued *Red data book* species.

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